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Population dynamics of red kangaroos (*Macropus rufus*) in relation to rainfall in the South Australian pastoral zone

S.C. CAIRNS* and G.C. GRIGG†

School of Biological Sciences, University of Sydney, New South Wales, 2006, Australia

Summary

1. Populations of red kangaroos (*Macropus rufus*) in the 282 000 km^2 pastoral zone of South Australia were assessed by aerial surveys conducted each year in winter for the period 1978–88, inclusive. The results of these surveys are used in a kangaroo management programme, the basis of which is the control of kangaroo numbers through regulated culling.

2. Rainfall in the pastoral zone is generally low and unreliable. Comparatively good seasons, with rainfall near to, or above average prevailed from 1978 to 1981. During this period, red kangaroo numbers increased throughout the pastoral zone. A drought occurred between 1982 and 1983. Associated with this drought was a dramatic decline in red kangaroo numbers; to the lowest level since 1978. Following the drought, the populations recovered, with steady increases in numbers from 1984 onwards.

3. The changes in red kangaroo numbers, in the form of the yearly exponential rate of population increase (r) were found to correlate best with intervals of rainfall at short time-lags from the second of any two successive aerial surveys used to determine r.

4. The numerical response of the red kangaroo populations to rainfall was investigated. Asymptotic models in the form of the negative exponential Mitscherlich equation were fitted to data for the period 1978–84. The rainfall input into these models was that for the calendar summer–autumn period between successive aerial surveys (January–June).

5. The response to summer–autumn rainfall in the Western region of the pastoral zone was different to that in the Central & Eastern region. Separate numerical response models were derived for each of these two regions. These models implied positive rates of exponential population growth ($r > 0$) when summer–autumn rainfall exceeded 74 mm in the Western region and 107 mm in the Central & Eastern region. They also implied maximum levels of r of 0·92 in the Western region and 0·38 in the Central & Eastern region.

6. Predictions by the numerical response models of the changes in red kangaroo numbers in relation to summer–autumn rainfall for the period 1984–88 proved to be rather poor, particularly for the years immediately following the drought. It is suggested that the reason for this was that the age structures and sex ratios of the post-drought populations were different from those of the populations used to develop the models. Drought is thought both to truncate the age structures of kangaroo populations and to bias the sex ratios towards the females. A result of this could be an increase in the numerical response to rainfall above that of a population near to the carrying capacity of its environment and with a near-stable age structure.

Key-words: red Kangaroo, population dynamics, numerical response, drought, aerial survey.

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* Present address: Department of Zoology, University of New England, Armidale, New South Wales, 2351, Australia.

† Present address: Department of Zoology, University of Queensland, Queensland, 4072, Australia.

Introduction

It is generally recognized that herbivore populations are closely aligned with food availability (Caughley & Lawton 1981) and that in arid and semi-arid rangeland systems this food availability, in the form of the amount of available plant biomass, is closely modulated by rainfall (Rosenzweig 1968; Fitzgerald & Nix 1970; Phillipson 1975; Robertson 1987a,b; Wellard 1987). Thus, an identifiable nexus exists between herbivore populations and rainfall in these rangeland systems. This nexus is manifest in a number of forms: the association between herbivore standing crop biomass and rainfall (e.g. Coe, Cumming & Phillipson 1976; East 1984); the association between the demographic processes which result in changes in herbivore numbers and rainfall (e.g. Sinclair 1977; Sinclair, Dublin & Borner 1985; J. Caughley, Bayliss & Giles 1984; Bayliss 1985a,b, 1987; Oxley 1987); and the association between secondary (animal) productivity and rainfall (e.g. Coe, Cumming & Phillipson 1976; Oxley 1987).

Until recently, most documented examples of associations between herbivore populations and rainfall were of ungulate populations. The establishment in Australia in the late 1970s of aerial survey programmes to monitor kangaroo populations (Caughley, Sinclair & Grigg 1979; Caughley & Grigg 1981, 1982) led to analyses of the association between changes in kangaroo numbers and rainfall at both a local scale (Bayliss 1985a,b, 1987) and a wider, regional scale (J. Caughley *et al.* 1984). An examination of the results of aerial surveys conducted on the western plains of New South Wales led J. Caughley *et al.* (1984) to propose curvilinear models to describe changes in kangaroo numbers in relation to regional rainfall. Following this, Bayliss (1985a) examined in detail the association between changes in kangaroo numbers and rainfall at Kinchega National Park in western New South Wales; proposing numerical response functions that related these changes to both rainfall and total standing crop of potentially edible plants (Bayliss 1985b, 1987).

In the South Australian pastoral zone, there are three species of large kangaroo that are commonly found: the red kangaroo, *Macropus rufus* (Desmarest), the western grey kangaroo, *M. fuliginosus* (Desmarest), and the euro or wallaroo, *M. robustus* Gould. Of these three species, the red kangaroo is the most widespread and abundant, being found throughout the whole of the pastoral zone (Cairns, Pople & Grigg 1991).

As in other parts of Australia of agricultural and pastoral importance, kangaroos in the South Australian pastoral zone are generally regarded as pests. Contingent to this, the South Australian National Parks and Wildlife Service (SANPWS) administers a kangaroo management programme, the basis of which is the control of kangaroos through regulated culling. As part of this programme, regular, annual surveys of the kangaroo populations of the South Australian pastoral zone have been conducted since 1978. Using results from these surveys, the present study documents the broad distributions of red kangaroos throughout the pastoral zone, their population trends over a period of 10 years, 1978–88, and examines the association between yearly changes in red kangaroo numbers and rainfall. In examining this association, a numerical response function is derived using data for the period 1978–84 and its suitability to other, later situations discussed.

Study area

The South Australian pastoral zone is approximately 282 000 km^2 in area and comprises about 25% of that state. It extends from the New South Wales and Victorian borders in the east, onto the Nullabor Plain in the west, and from the Eyre Peninsula in the south to Coober Pedy in the north. It is bounded in the east, the north and the west by a vermin-proof fence. Significant landmarks of the pastoral zone include the Flinders Ranges and several large salt lakes. These aside, the basic landforms of the pastoral zone comprise plains, undulating plains, flood plains and sand dune fields. Structurally, the native vegetation comprises mainly tall and low shrublands, and some low woodlands. Mallee woodlands occur in the southern parts of the pastoral zone. Most of the shrublands are dominated by the chenopod shrubs bluebush (*Maireana* spp.) and saltbush (*Atriplex* spp.). Detailed description of the pastoral zone environment is given by Laut *et al.* (1977). The associations that exist between kangaroos and the different landforms, soils and vegetation types are discussed in Cairns *et al.* (1991).

Rainfall in the pastoral zone is generally low and highly unreliable. In the south it is seasonal with a winter peak; in the north it is non-seasonal (Division of National Mapping 1986). There is a marked latitudinal gradient in mean annual rainfall, ranging from *c.* 400 mm on the Eyre Peninsula to <150 mm in the north-west. Evaporation is high and, along with temperature, increases with decreasing latitude.

The most common form of land use in the pastoral zone is extensive livestock grazing. In some areas in the south, land use extends to more intensive grazing, grain growing and horticulture. On average, the area supports about 2·5 million sheep and 90 000 cattle (McBride 1983).

For the purpose of kangaroo management, the pastoral zone has been subdivided by SANPWS into 10 zones based broadly upon environmental divisions of the area given by Laut *et al.* (1977). This subdivision is shown in Fig. 1; the areas of each zone are

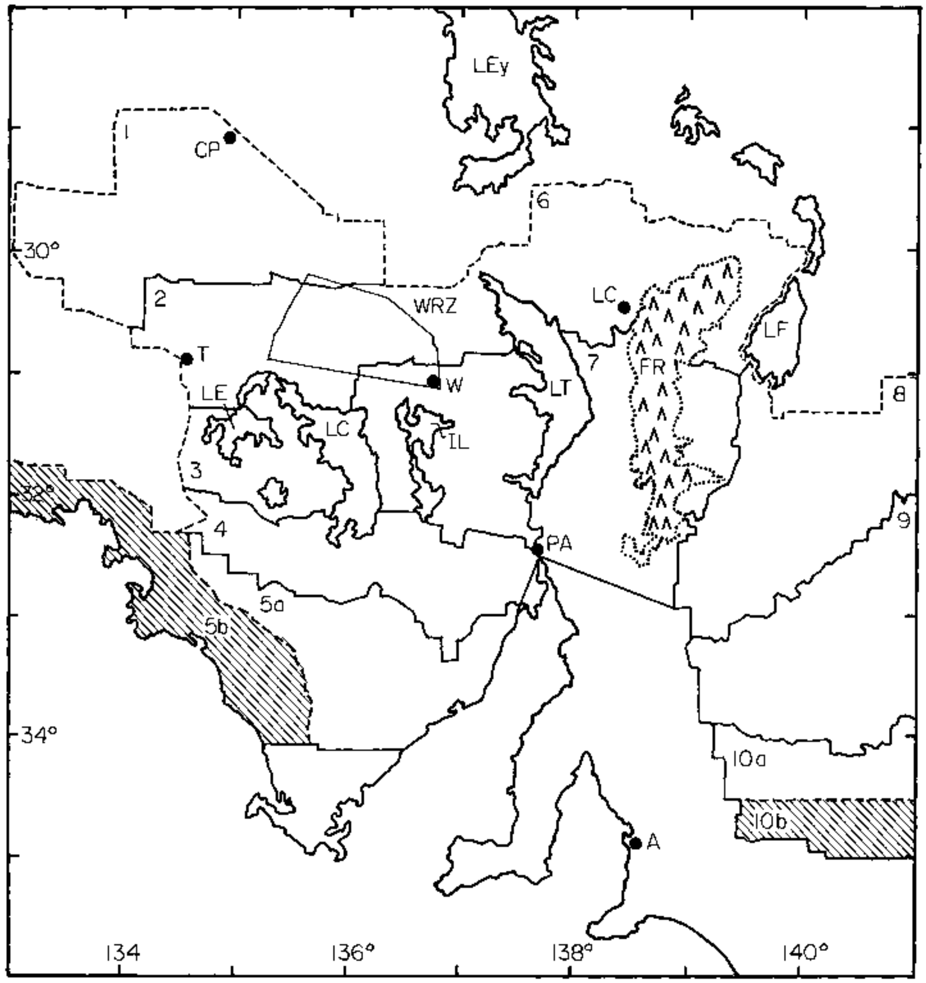

Fig. 1. The pastoral zone of South Australia showing the SANPWS kangaroo management zones. The hatched areas were not surveyed. The vermin-proof fence which bounds the pastoral zone in the north and the west is shown as a dashed line. Other geographical features are coded by the following abbreviations: A, Adelaide; CP, Coober Pedy; FR, Flinders Ranges; IL, Island Lagoon; LC, Leigh Creek; LE, Lake Everard; LEy, Lake Eyre; LF, Lake Frome; LG, Lake Gairdner; LT, Lake Torrens; PA, Port Augusta; T, Tarcoola; W, Woomera; WRZ, Woomera Restricted Zone.

given in Table 1. These management zones form the areal base upon which kangaroo numbers were estimated.

Methods

POPULATION ESTIMATES

Using what has become the standard method of aerial survey for kangaroos (Caughley, Sinclair & Scott-Kemmis 1976; Caughley 1977; Caughley & Grigg 1981), the red kangaroo populations of the pastoral zone were surveyed annually from 1978 to 1988, inclusive. The first two surveys, conducted in 1978 and 1979, were each carried out in two stages, the first in late winter and the second in early spring (Caughley & Grigg 1981). All subsequent surveys have been conducted during late winter (late July–early August). With the large salt lakes and those parts of the Flinders Ranges above the 500 m contour excluded, the total area that could be surveyed was 245 400 km^2. The Woomera Restricted Area (a former rocket testing range) of management zones 2 and 3 (Fig. 1) was not surveyed before 1984. The whole of management zone 5a was surveyed in 1983, 1984 and 1985 only, while management zone 10a was surveyed in all years except 1988. Management zones 5b and 10b did not constitute part of the survey.

Surveys were conducted along east–west transects spaced at intervals of 28 km across the pastoral zone (see Fig. 1 in Caughley & Grigg 1981). A high-winged aircraft (Cessna 182) was flown along the transect lines at a speed of 185 km h^{-1} (100 kts), 76 m (250 ft) above the ground. Two observers, each seated on opposite sides of the aircraft, scanned a 200-m wide strip of ground delineated by markers on the aircraft's struts. Airspeed was adjusted to account for wind so that 5 km were traversed every 97 s. This period was followed by a 7 s break, during which observers recorded the number of kangaroos seen. Overall sampling intensity was 1·3% (Caughley & Grigg 1981).

Surveys were conducted within 3–4 h of sunrise

Table 1. The areas, the long-term average annual rainfalls and the number of rainfall recording stations (n) in the SANPWS kangaroo management zones

Kangaroo management zone	Area (km^2)	Average annual rainfall (mm)	n
1	38 900	170	11
2	23 600	175	8
3	27 400	190	11
4	24 300	230	10
5a	19 500	—	—
6	26 600	200	15
7	20 200	300	26
8	33 700	230	24
9	22 600	220	5
10a	8 600	315	12
Total	245 400	—	—

or sunset. Because observers do not see all the animals present on the survey strip, correction factors were applied to the counts of red kangaroos. This has been done primarily for the purpose of providing SANPWS with estimates of kangaroo numbers for its management programme. The correction factors used were those derived by Caughley, Sinclair & Scott-Kemmis (1976). For open country, counts were multiplied by a factor of 2·29; for lightly wooded country, counts were multiplied by 2·36; for more heavily wooded country, counts were multiplied by 2·43.

RAINFALL

Monthly records of rainfall were obtained from the Australian Bureau of Meteorology for all recording stations in the pastoral zone for the period 1975–88. From these records, average quarterly total rainfalls were calculated for each of the kangaroo management zones. Some zones are better served by recording stations than others (Table 1). Long-term (40–100 years) monthly average rainfalls were also obtained from the records and used to determine the long-term average annual rainfalls for the management zones (Table 1).

DATA AND STATISTICAL ANALYSES

The densities and total numbers of kangaroos in each of the management zones were determined from the survey results by the ratio method of estimation (Cochran 1963; Caughley 1977). A full description of the application of this method is given in Caughley & Grigg (1981).

To determine the form of the numerical response function in relation to rainfall, yearly changes in red kangaroo numbers in the different SANPWS kangaroo management zones were correlated with different intervals of rainfall. While the numerical response function may not be linear, it was nevertheless assumed that the linear approximation of the correlation would indicate which intervals of rainfall were best related to the yearly changes in red kangaroo numbers. This analysis was conducted using data from eight of the ten kangaroo management zones. Management zones 5a and 10a were excluded from all analyses; the former because of the dominance of farming as a land use and the limited number of survey estimates, and the latter because of agricultural land use and low kangaroo numbers.

Changes in red kangaroo numbers were determined as the yearly (August–July) exponential rates of population increase (r): the natural logarithm of the ratios of successive estimates of kangaroo density. This rate of population increase was used because it is the per capita rate of increase of simple models of population growth (Krebs 1978), and because its use would allow comparisons to be made between the findings of this study and other similar studies on kangaroos (J. Caughley *et al.* 1984; Bayliss 1985a,b).

The calculated yearly exponential rates of population increase (r) were correlated with rainfall for intervals of 3, 6 and 12 months, at increasing time-lags set from the second of any two successive aerial surveys. The time-lags used ranged, in steps of 3 months, from 3 to 24 months. Although not included in the analysis because at least half of it extends past the pivotal, second aerial survey, the 3 month interval with a zero time-lag is the July–September interval. In accordance with this, the 3-month interval lagged 3 months is the calendar autumn period (April–June) between successive surveys; the 6-month interval lagged 3 months is the calendar summer–autumn period (January–June) between successive surveys; and the 12-month interval lagged 3 months is that summer–autumn interval plus the preceding calendar winter–spring interval of July–December. The linearity or otherwise of the associations between r and the different intervals of rainfall was assessed further by the examination of bivariate plots.

Since there must be a limit to the rate at which a population can increase in relation to the availability of a resource, it was anticipated that the form of the numerical response function would probably be asymptotic. There are a number of models that suitably represent such asymptotic relationships (Noy-Meir 1978; May 1981). Of these, the one selected for the numerical response function was the Mitscherlich equation (Ratkowsky 1983). Preliminary testing of the data with this and another model, the Michaelis-Menten equation, led to this selection. As was suggested by Bayliss (1987), this model also appears to be less sensitive to outlying data points. In its general form, the Mitscherlich equation is an inverted exponential function and has the formula:

$$r = a - b\exp(-kV) \qquad \text{eqn 1}$$

where V is the rainfall during the selected time interval, and a, b and k are constants. This model was fitted to data for the period 1978–84 using the method of maximum likelihood estimation and the MLP program (Ross 1980). Its generality was then tested by comparison with the demographic events of the subsequent period 1985–88. The mean square error of prediction (MSEP) proposed by Wallach & Goffinet (1989), the average squared difference between the quantity of interest and the model prediction of that quantity, was used as a statistic in this evaluation.

Results

DISTRIBUTION AND VARIABILITY IN RED KANGAROO NUMBERS

Red kangaroos were present in all 10 of the SANPWS kangaroo management zones. Average densities ranged from $11{\cdot}3\,km^{-2}$ in management zone 8, to $0{\cdot}2\,km^{-2}$ in management zone 5a (Table 2). Temporal variation in the northern management zone (numbers 1–3 and 6–8) was high, but reasonably uniform at 30–50%. In two of the southern zones (numbers 4 and 9) which had characteristically low densities, it was uniformly lower at <30%. In zone 10a, red kangaroo densities were low and highly variable.

In terms of these average densities, the SANPWS kangaroo management zones could be considered comprising three broad groups (zones 5a and 10a excluded): one in the north-west with medium densities (zones 1–3), one in the north-east with relatively high densities (zones 6–8), and one in the south with low densities (zones 4 and 9).

TRENDS IN RED KANGAROO NUMBERS AND VARIATIONS IN RAINFALLS

The densities of red kangaroos in the SANPWS kangaroo management zones for the 10-year period of the study, 1978–88, are shown in Fig. 2. The corresponding numbers in each management zone are given in Appendix 1. Total numbers for the whole pastoral zone (zone 5a excluded), along with the overall percentage changes in these numbers, are given in Table 3.

Rainfalls for the calendar summer–autumn (hatched) and winter–spring periods of the years 1977–88 for the eight kangaroo management zones where red kangaroos are abundant are shown in Fig. 3. A feature of these rainfalls is their considerable spatial and temporal variation. Spatial variation was greatest in the two management zones associated with the Flinders Ranges, zones 6 and 7. However, while average variation in rainfall within the eight management zones was in the range 15–30% (CV%), it was highest during 1982; the first year of the drought (see also Fig. 4 in Cairns *et al.* 1991).

Between 1978 and 1981, red kangaroo numbers increased throughout the pastoral zone. In management zones 4, 9 and 10a, where densities were characteristically low (Table 2), these increases were only moderate. In both the north-western management zones (numbers 1–3) and the north-eastern management zones (numbers 6–8), the increases were quite substantial (Fig. 2); particularly between 1980 and 1981, during which time total red kangaroo numbers almost doubled (Table 3). Coincident with these increases in numbers were rainfalls that were 20–50% above the regional long-term averages between 1978 and 1980, and near average between 1980 and 1981 (Fig. 3).

Following on from this period of population growth was one of population decline. Between the 1981 and 1982 aerial surveys, the total number of red kangaroos in the pastoral zone was found to have declined markedly (Table 3). This decline,

Table 2. Average densities, and the coefficients of temporal variation (CV%) of these densities, of red kangaroos in the SANPWS kangaroo management zones for the period 1978–88

Kangaroo management zone	Red kangaroo density (km^{-2})	CV (%)
1	3·33	30·1
2	5·07	48·7
3	4·16	31·1
4	1·58	23·6
5a	0·19	—
6	7·01	52·9
7	7·55	41·5
8	11·32	41·8
9	2·58	30·5
10a	0·31	136·1

Table 3. The total numbers of red kangaroos (±SE) in the South Australian pastoral zone and the annual percentage changes in these numbers in relation to the previous year for the period 1978–88. The numbers of red kangaroos in management zone 5a have not been included in these estimates, nor have the numbers in management zone 10a for the years 1987 and 1988. The percentage changes have been adjusted accordingly

Year	Number of red kangaroos	% change
1978	1 000 000 ± 64 300	—
1979	1 119 500 ± 63 100	+12
1980	1 137 600 ± 86 500	+16
1981	2 175 200 ± 115 000	+91
1982	1 363 600 ± 99 300	−37
1983	804 600 ± 53 700	−41
1984	745 100 ± 40 900	−7
1985	1 139 700 ± 95 500	+53
1986	1 129 900 ± 73 300	−1
1987	963 300 ± 49 500	−15
1988	1 457 000 ± 92 300	+51

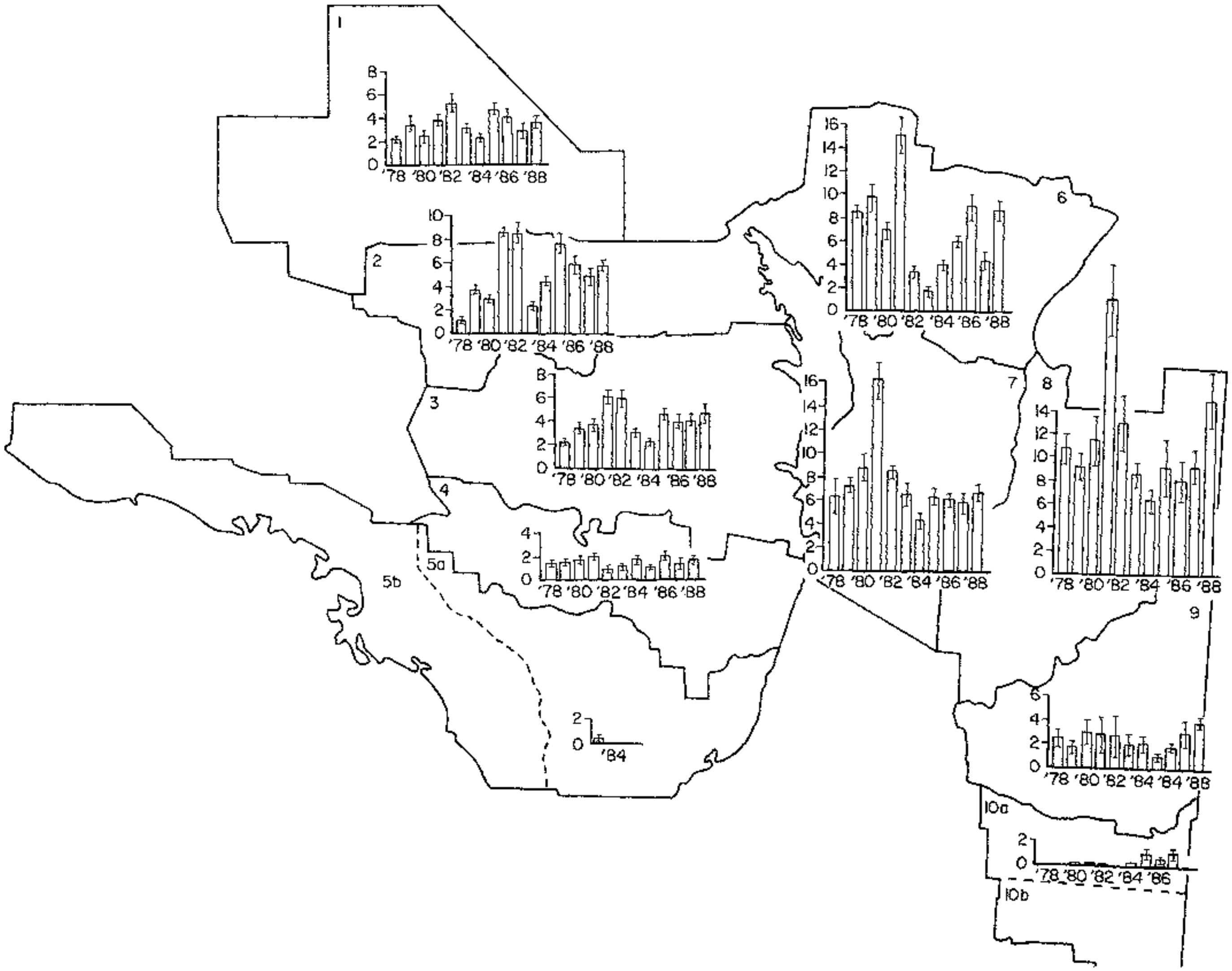

Fig. 2. Densities (±SE) of red kangaroos (km^{-2}) in the SANPWS kangaroo management zones for the years 1978–88. All management zones were surveyed each year with the exception of zones 5a, which was surveyed in the years 1983–85 only, and 10a, which was surveyed in all years except 1988. Kangaroo management zones 5b and 10b were not part of the survey.

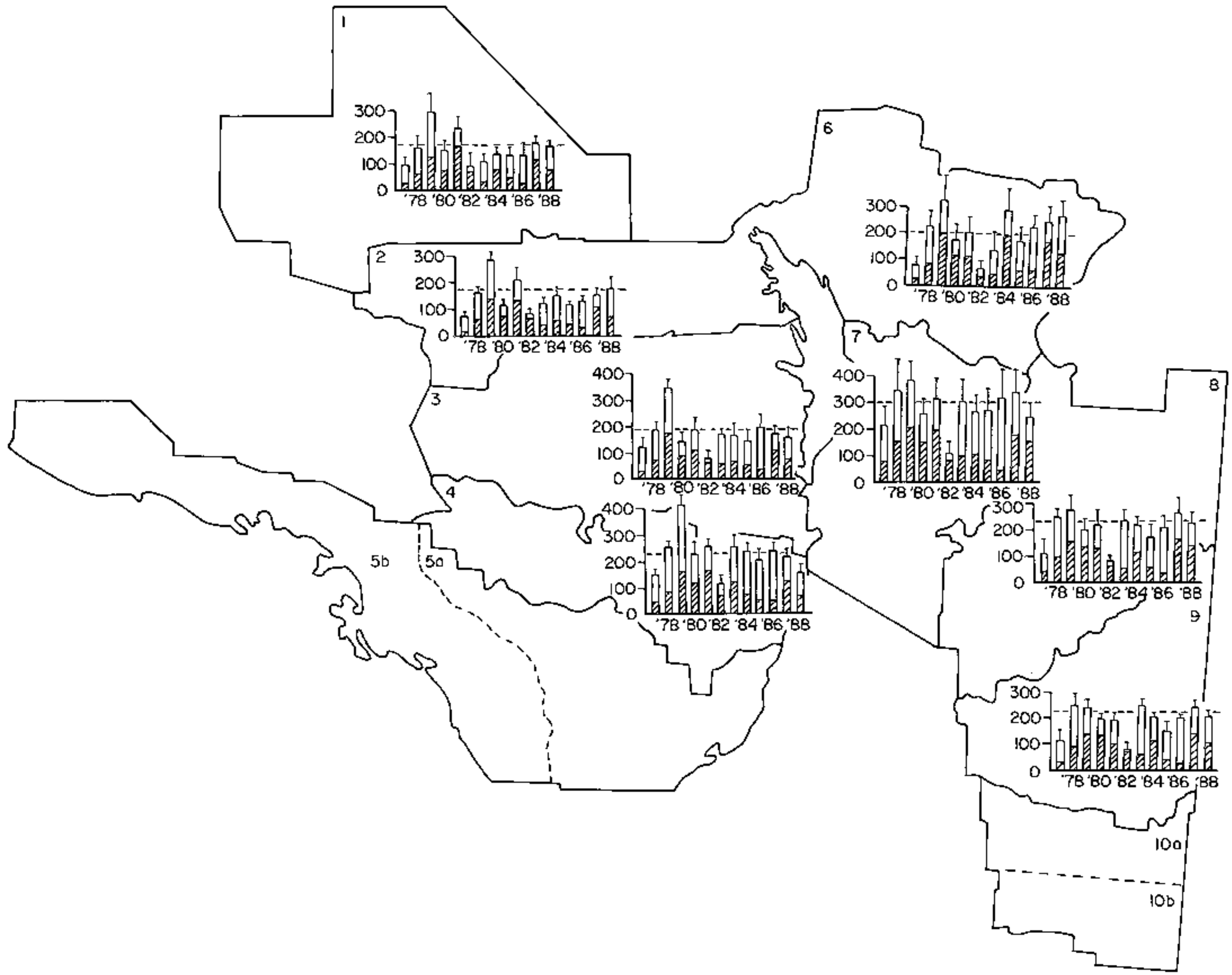

Fig. 3. Average rainfalls (mm) in the SANPWS kangaroo management zones (zones 5 and 10 excluded) for the summer–autumn (hatched) and winter–spring periods of the years 1977–88. The error bars represent 1 SD of total annual rainfall. The dashed horizontal line represents the long-term annual average rainfall for each management zone.

however, was not uniform throughout the pastoral zone (Fig. 2). The same was the case for the below-average rainfalls recorded during this period (Fig. 3).

In the north-east of the pastoral zone, rainfall recorded between the 1981 and 1982 aerial surveys was 33% below the long-term average. Associated with this was a general decline of 54% in red kangaroo numbers in management zones 6–8. In the south (zones 4 and 9), rainfall for this period was 24% below the long-term average. Associated with this was a 27% decline in the number of red kangaroos across both management zones. In the north-west, rainfall for this period was, at 22%, below the long-term average, comparable to that in the south. Associated with this, however, and contrary to what had occurred in the other parts of the pastoral zone, was a small increase (8%) in the number of red kangaroos in management zones 1–3. These events were all coincident with the beginning of the drought in eastern Australia (see Caughley, Grigg & Smith 1985).

Between the 1982 and 1983 aerial surveys, red kangaroo numbers declined further throughout the pastoral zone (Table 3). This time though, the decline was more widespread than it was in the previous year, occurring in both the north-eastern and north-western management zones, and in one of the two southern management zones (Fig. 2). Rainfalls for this period were also below average (Fig. 3). In the north-east of the pastoral zone, rainfall was 63% below the long-term average. Associated with this was a further decline of 32% in red kangaroo numbers in management zones 6–8. In the north-west, it was similarly low at 64% below the long-term average. The corresponding decline in the number of red kangaroos in management zones 1–3 was a substantial 55%. In the south, rainfall was 49% below the long-term average. Associated with this, however, was a decline in red kangaroo numbers of only 17%.

In assessing the impact of the drought on the red kangaroo populations in the different regions of the pastoral zone, a single-factor repeated measures analysis of variance (Winer 1971) was conducted on the yearly rates of population decline (as measured by r) in the north-east, the north-west and the south of the pastoral zone. In this analysis, the kangaroo management zones of these regions were the replicates and the repeated measures were the values of r for 1982 and 1983. The result of this analysis was a significant region by year interaction ($F = 7{\cdot}89$ on 2,5 df; $P < 0{\cdot}05$), indicating initially that the impact of the drought between 1981 and 1983 was not uniform throughout the pastoral zone. Further analyses, in the form of the examination of the simple main effects (Winer 1971), showed that there was a significant difference between the rates of decline in 1982 and 1983 in both the north-east ($F = 17{\cdot}70$ on 1,5 df; $P < 0{\cdot}01$) and north-west ($F = 21{\cdot}86$ on 1,5 df; $P < 0{\cdot}01$) of the pastoral zone, but not in the south ($F = 0{\cdot}95$ on 1,5 df; $P > 0{\cdot}50$). Also, there were significant differences among the rates of decline in the three regions in 1982 ($F = 5{\cdot}37$ on 2,12 df; $P < 0{\cdot}05$), but not in 1983 ($F = 2{\cdot}73$ on 1,5 df; $P > 0{\cdot}10$).

The arrival of good winter rainfalls in the east of the pastoral zone in 1983 signalled the breaking of the drought (see Caughley *et al.* 1985). Between the 1983 and 1984 aerial surveys, rainfalls that were 28% and 17% above average were recorded in the north-east and south of the pastoral zone, respectively. In the north-west, however, the rainfall for this period was 13% below average. Associated with these rainfalls was a further 16% decline in red kangaroo numbers in the north-east, virtually no change in numbers in the north-west, and a 29% increase in numbers in the south. By 1984, the total number of red kangaroos in the pastoral zone had reached its lowest level since aerial surveys had begun in 1978. It had declined to 34% of the 1981 peak of 2·15 million red kangaroos (Table 3).

Between the 1984 and 1985 aerial surveys, regional rainfalls were 22–26% below average (Fig. 3). Associated with this was an overall increase of 53% in the number of red kangaroos (Table 3). Although the rainfalls for this period were relatively uniform, the changes in kangaroo numbers at the regional level were not. Numbers increased by 51% in the north-east, and by 91% in the north-west. In the south, however, the opposite occurred, with numbers decreasing by 44%.

Between 1985 and 1986, and again between 1986 and 1987, there were small overall declines in the total number of red kangaroos in the pastoral zone (Table 3). As on previous occasions, these declines were not uniform throughout the pastoral zone (Fig. 2). Also as on previous occasions, nor were the corresponding regional rainfalls uniform throughout the pastoral zone (Fig. 3). In the north-east, a 6% increase in red kangaroo numbers between 1985 and 1986 was associated with rainfall that was 22% below average, while a 16% decline in numbers between 1986 and 1987 was associated with rainfall that was 57% above the average. In the north-west, a 17% decline in the number of red kangaroos between 1985 and 1986 was associated with rainfall that was 26% below average, while a 20% decline in numbers between 1986 and 1987 was associated with rainfall that was 38% above average. In the south, a 74% increase in red kangaroo numbers between 1985 and 1987 was associated with rainfall that was 24% below average, while a 14% decline in numbers between 1986 and 1987 was associated with rainfall that was 27% above the average.

Between 1987 and 1988, the total number of red kangaroos increased by 51%. In the north-east, a 70% increase in numbers was associated with average regional rainfall. Increases in numbers of 33% and 26% were associated with regional rainfalls that were 26% and 18% below average in the north-west and south, respectively.

ASSOCIATION BETWEEN RED KANGAROO NUMBERS AND RAINFALL

The correlations between r and rainfall for intervals of 3, 6 and 12 months with successive 3-month time-lags for eight of the ten kangaroo management zones are summarized in Table 4. The strongest positive, and most consistent, correlations between r and all three intervals of rainfall were found to be at the shortest of the time-lags. Successive increases in the time-lags resulted in the correlations becoming weaker and more variable up to lags of 21 months in the cases of the 3 and 6-month intervals, and 18 months in the case of the 12-month interval. At these points a second, but quite variable, peak occurred. Between 1984 and 1985, red kangaroo numbers increased in six of the eight management zones; zones 4 and 9 being the exceptions (Fig. 2). This was despite the fact that regional rainfalls for this period were generally below average (Fig. 3). In the years prior to 1985, numbers had increased with rainfalls which were average or above, and decreased under conditions of below average rainfall. Exclusion of 1985 from the analyses, on the basis that it was a possible outlier year, resulted in a strengthening (of the order of 10–25%) of the correlations between r and rainfall at the short time-lags of 3 and 6 months.

Further to the correlation analyses, examination of the plots of r against the various lagged intervals of rainfall indicated that in some cases the relationship between these two factors was perhaps asymptotic rather than linear. This was particularly so for the case of r and rainfall for the 6-month interval with a 3-month time-lag; the calendar summer–autumn period between successive surveys (January–June). A numerical response function in the form of a

Table 4. Mean correlation (±SD) between the yearly exponential rates of population increase (r) and intervals of rainfall at different time-lags for red kangaroos in the SANPWS kangaroo management zones. Management zones 5a and 10a were excluded from the analyses (see text)

Time-lag (months)	Interval of rainfall (months)		
	3	6	12
3	0·42 ± 0·18	0·38 ± 0·15	0·41 ± 0·15
6	0·13 ± 0·20	0·13 ± 0·15	0·26 ± 0·14
9	0·06 ± 0·19	0·05 ± 0·18	0·16 ± 0·20
12	0·03 ± 0·16	0·14 ± 0·31	0·08 ± 0·26
15	0·14 ± 0·31	0·08 ± 0·26	0·16 ± 0·32
18	−0·05 ± 0·25	0·10 ± 0·32	0·26 ± 0·33
21	0·28 ± 0·42	0·33 ± 0·33	0·18 ± 0·29
24	−0·28 ± 0·24	0·15 ± 0·21	0·16 ± 0·31

Mitscherlich equation was fitted to r and rainfall for this time interval for the period 1978–84; a period which included a wide range of summer–autumn rainfalls. In fitting this model, the eight management zones were divided into two groups based upon their long-term average annual rainfalls (Table 1). One of these groups, the Western kangaroo management zones, comprised management zones 1–3 and had long-term average annual rainfalls <200 mm. The other group, the Central & Eastern kangaroo management zones, comprised management zones 4, 6–9 and had long-term average annual rainfalls >200 mm. Average red kangaroo densities in the Western management zones were in the range 3–5 km^{-2} while in the Central and Eastern management zones they were in the much broader range 1–11 km^{-2} (Table 2). Fitting separate Mitscherlich equations to each of the two groups of management zones resulted in a significant reduction in the error mean square when compared to fitting a single model for all eight management zones ($F = 3{\cdot}23$ on 3,42 df; $P < 0{\cdot}05$).

In terms of the approximate percentages of variance accounted for by these two models (R^2), the two Mitscherlich equations proved better representations of the numerical response function of the red kangaroos populations to rainfall than did simple linear regressions. For the Western management zones, R^2 was 54% for the Mitscherlich equation, compared to 46% for the linear regression. For the Central & Eastern management zones, R^2 was 52% for the Mitscherlich equation, compared to 43% for the linear regression. Quadratic regression did not fit these data. The coefficients for the two Mitscherlich equations are given in Table 5; the forms of these numerical response functions in relation to the data from which they were derived are shown in Fig. 4.

Two features of the fitted models shown in Fig. 4 are worth noting. The first of these is the minimum amount of summer–autumn rainfall required before an increase would occur in the 'observable' red kangaroo population ($r > 0$). This was estimated at 74 mm for the Western management zones, and 107 mm for the Central & Eastern management zones. The second feature is the asymptotic maximum of r represented by the parameter 'a' of the Mitscherlich equation (Table 5). For the Western management zones, this was a particularly high value of 0·92, while for the Central & Eastern management zones it was much lower at 0·38.

The extent to which these models represent the general relationship between changes in red kangaroo numbers (as measured by r) and summer–autumn rainfall in the South Australian pastoral zone was assessed by evaluating them against the demographic events of 1984–88. Figure 5 shows values of r for the period 1984–88 in relation to both the summer–autumn rainfalls for that period

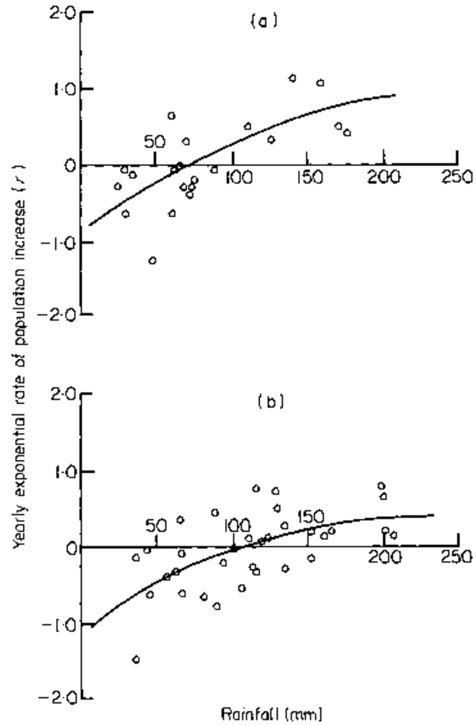

Fig. 4. The numerical responses (Mitscherlich equations) of red kangaroo populations (1978–84) to summer–autumn rainfall in (a) the Western kangaroo management zones (numbers 1–3) and (b) the Central & Eastern kangaroo management zones (numbers 4, 6–9).

and the numerical response models that were derived using data for the period 1978–84. Some of the relationships between r and summer–autumn rainfall for this period were found to be at considerable variance to the models. Examination of the mean square error of prediction (MSEP) for the 4-year period 1984–88 confirms this (Table 6). However, it also shows that, as the perturbating effect of the drought receded with time, the values of the MSEP decreased; from peak values in 1985 in the case of the Western management zones, and in 1986 in the case of the Central & Eastern management zones. The subsequent relationships between r and summer–autumn rainfall appeared to be similar to those represented by the two models (Fig. 5).

Table 5. The coefficients (±SE) for the Mitscherlich equations of r for red kangaroos versus summer–autumn rainfall, fitted to data from the Western and Central & Eastern groups of kangaroo management zones. Also given are the approximate percentages of variance accounted for by the respective models (R^2)

	Mitscherlich equation: a	b	$r = a - b\exp(-kV)$ k	R^2
Western	0·92 ± 0·57	2·98 ± 1·05	0·016 ± 0·012	54%
Central & Eastern	0·38 ± 0·24	2·90 ± 1·05	0·019 ± 0·009	53%

Table 6. The mean squared errors of prediction (MSEP) for the Mitscherlich equations fitted to the red kangaroo populations in the Western and the Central & Eastern kangaroo management zones for the years 1978–84 in relation to changes in those populations in the years 1985–88

Year	Western	Central & Eastern
1985	1·234	0·489
1986	0·609	1·607
1987	0·468	0·218
1988	0·071	0·153

Discussion

The present study extended over a period of 10 years, 1978–88. The most critical event of this period was a drought with which there was associated a substantial decline in red kangaroo numbers in the South Australian pastoral zone between 1981 and 1984 (Table 3). This drought extended throughout much of south-eastern Australia (Caughley *et al.* 1985); resulting in declines in kangaroo numbers in both western New South Wales (J. Caughley *et al.*

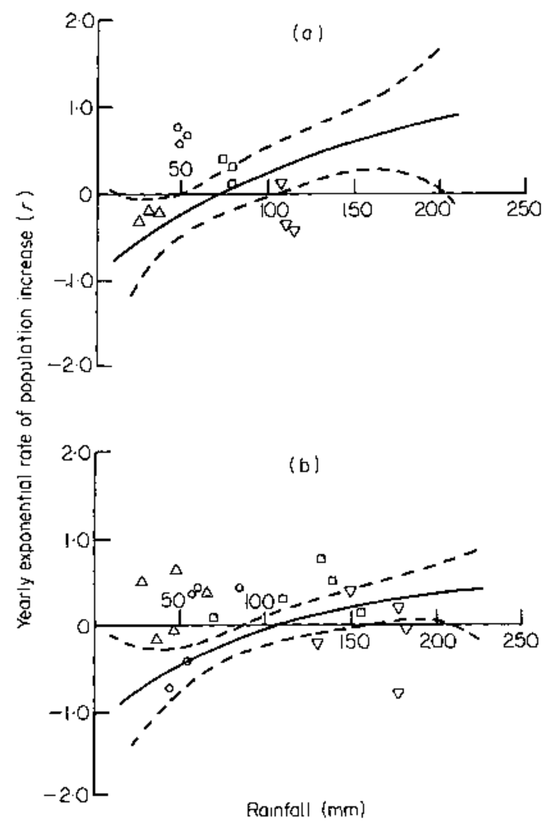

Fig. 5. The numerical responses of red kangaroo populations to summer–autumn rainfall for the years 1985–88 in (a) the Western kangaroo management zones (numbers 1–3) and (b) the Central & Eastern kangaroo management zones (numbers 4, 6–9). These numerical responses are shown in relation to the numerical response curves for the years 1978–84 (see Fig. 4). The dashed lines represent the approximate 95% confidence intervals about the curves. ○, 1985; △, 1986; ▽, 1987; □, 1988.

1984) and south-western Queensland (Caughley *et al.* 1985), as well as in South Australia. In examining the broad scale effect of the drought between April 1982 and March 1983, Caughley *et al.* (1985) concluded that the rates of decline in kangaroo numbers throughout the inland plains of New South Wales, South Australia and southern Queensland were relatively uniform, and therefore independent of kangaroo density. This was attributed to the apparent speed with which the drought intensified following its onset; overriding any effect of grazing on the rate at which plant biomass declined (Caughley *et al.* 1985). Events in the South Australian pastoral zone did not entirely conform to this model. With the onset of the drought in 1982, red kangaroo numbers declined substantially in the north-east of the pastoral zone. In the north-west, where numbers before the drought were less than half those in the north-east, no such decline occurred (Fig. 2). However, as the drought deepened between 1982 and 1983, declines in red kangaroo numbers which were independent of density, did occur throughout the pastoral zone.

As had been found in other studies (J. Caughley *et al.* 1984; Bayliss 1985a,b), the changes that occurred in red kangaroo numbers in the South Australian pastoral zone have been found to be correlated with lagged intervals of rainfall. In a study conducted at Kinchega National Park in the semi-arid rangelands of western New South Wales, Bayliss (1985a,b) found that seasonal yearly changes (winter–winter, spring–spring, etc.) in both red and western grey kangaroo numbers were positively correlated with a number of lagged intervals of rainfall; some of these correlations being stronger than others. On the basis of this, Bayliss (1985a,b) proposed that a 12-month interval of rainfall with a 6-month time-lag from the mid-point between successive seasonal aerial surveys was an 'appropriate and convenient' index of kangaroo food supply to which seasonal yearly changes in kangaroo numbers could be related. Paradoxically, the reference to this particular interval of rainfall as an 'appropriate and convenient' index of kangaroo food supply was despite the fact that plant biomass at Kinchega was strongly correlated with rainfall for the previous 6 months (Robertson 1987a,b). J. Caughley *et al.* (1984) also used this particular interval of rainfall as an index of kangaroo food supply in an analysis of the kangaroo populations of the western plains of New South Wales; the populations in that study being surveyed on a winter–winter basis only.

The yearly changes that occurred in red kangaroo numbers in the South Australian pastoral zone between 1978 and 1988 were found to be positively correlated with intervals of rainfall at short time-lags from the second of any two consecutive aerial surveys (Table 4). These intervals included, in part at least, rainfall from the period over which the changes in kangaroo numbers had occurred. This is a result not inconsistent with the associations found to exist at Kinchega between plant biomass and rainfall (Robertson 1987a,b), and between changes in kangaroo numbers and plant biomass (Bayliss 1987). The correlation between r and the interval of rainfall equivalent to Bayliss' (1985a,b) 'appropriate and convenient' index of kangaroo food supply was a much weaker one.

Although r was positively correlated with intervals of rainfall at short time-lags, the influence of rainfall would appear to be negatively biased; its absence having a greater impact than its occurrence. Caughley (1987) noted that a shortfall in rainfall will reduce a kangaroo population's rate of increase more than an excess of rainfall of the same magnitude will increase it; the rate of increase becoming negative with a severe shortfall of rainfall. The two population processes thought to contribute most to r, determined on such a large scale as in the present study, are mortality and effective natality (recruitment into the 'observed' population). While both could be considered to be continuous (instantaneous) processes, the actual mechanisms of their operation are open to a certain amount of speculation.

Concerning mortality in the 'observable' population, it is likely that its mechanism of operation is a simple one in that a broad scale shortage of available food, such as would occur in a drought, would lead to the deaths of the more vulnerable individuals in a population. Concerning effective natality, the process could be more complicated. Initial recruitment in the form of the production of pouch young, is almost an ongoing, non-seasonal process (Shepherd 1987). Under good seasonal conditions, the recruitment of pouch young into the 'observable' population should be a similar ongoing process. Under conditions of drought, however, both these processes can be interrupted; the first by females entering anoestrus (Newsome 1964), and the second either by pouch young failing to survive to the point of recruitment into the 'observable' population or by not surviving the process of weaning because of a diminished food supply (Newsome 1965; Shepherd 1987). Either way, the impact of drought conditions upon pouch young is such that older, larger individuals are more likely to suffer food deprivation and die than are younger, smaller individuals (Shepherd 1987). Although agreeing that mortality in kangaroo populations in semi-arid and arid rangelands and its detection by aerial survey is essentially instantaneous, Bayliss (1987) suggested that there is a time-lag in the detection of recruitment into the 'observable' population; the length of this time-lag depending upon seasonal condition. This time-lag was thought to be longer following a drought than during a period of good seasonal conditions (J. Caughley *et al.* 1984; Bayliss 1985a, 1987).

A factor contributing to some extent to the changes in red kangaroo numbers in the South Australian pastoral zone is commercial culling. Between 1978 and 1988, the proportion of the total population of red kangaroos in the pastoral zone culled has been in the range 6–13% (SANPWS, unpublished data). At present, more precise figures than these are not available. An inverse association existed between these proportions and red kangaroo numbers; the highest proportions being culled during the drought when numbers were lowest. Bayliss (1987) suggested that the effect on a population of culling it at a relatively low level, such as has occurred in the South Australian pastoral zone, will be negligible; particularly when compared to the effects that changing levels of food availability are likely to have upon it. Bayliss (1987) also suggested that culling sustained throughout a drought is probably only removing from a population those individuals that would not normally have survived the drought; harvest mortality being essentially a subset of total mortality. In the present study, both these assumptions have been made regarding the impact of culling upon changes in kangaroo numbers.

A POPULATION MODEL: THE NUMERICAL RESPONSE FUNCTION

Confronted with changes in the availability of resources, one of the responses elicited from consumers is a group or population response — a numerical response. Proposed by Solomon (1949) and Holling (1959, 1961) as a component of predator–prey relationships, the numerical response is due to changes in natality, mortality, immigration and emigration. More recently, the concept of the numerical response has been incorporated into the analysis of herbivore–resources interactions (Noy-Meir 1978; Caughley 1981; Caughley & Lawton 1981; Caughley & Krebs 1983). In a study conducted on the population dynamics of red and western grey kangaroos at Kinchega National Park, Bayliss (1985b, 1987) proposed explicit models for the numerical responses of kangaroo populations at Kinchega to resource availability in the form of standing plant biomass and to an index of resource availability in the form of a lagged interval of rainfall. J. Caughley *et al.* (1984) also proposed explicit models of changes in kangaroo numbers in relation to a lagged interval of rainfall.

In the present study, two explicit models in the form of the inverted exponential Mitscherlich equation have been proposed for the numerical response function of red kangaroo populations in the South Australian pastoral zone in relation to an index of resource availability in the form of summer–autumn rainfall (Fig. 4). These models were of the same general form as one of the three types proposed by Bayliss (1985b, 1987). The other two types of models proposed by Bayliss (1985b) were the ramp model and the rectangular hyperbola, the Michaelis-Menten equation. Bayliss (1987) had found the Mitscherlich equation to be a more suitable and tractable model than a model such as the Michaelis-Menten equation because it was less sensitive to outlying data points. This was also found to be the case in the present study where a preliminary analysis using the Michaelis–Menten equation (Cairns, Pople & Grigg 1988) resulted in model parameters with proportionally much larger standard errors than those for the parameters of the Mitscherlich equation.

The general forms of the numerical response to a rainfall resource index was essentially the same for both red kangaroos in the South Australian pastoral zone (present study), and red and grey kangaroos in western New South Wales (J. Caughley *et al.* 1984; Bayliss 1985b, 1987). However, the rainfall indices of resource availability that elicited the numerical response were different. In western New South Wales it was found that, in relation to winter–winter aerial surveys, rainfall for the 12 months before the first of two successive aerial surveys was used as an 'appropriate and convenient' index of resource availability (J. Caughley *et al.* 1984; Bayliss 1985b, 1987). This was not the case for red kangaroos in the South Australian pastoral zone. It was the summer–autumn rainfall between successive winter aerial surveys that was found to be not only the most appropriate index of resource availability, but the most critical one in relation to survival and effective natality in these red kangaroo populations.

At the 'equilibrium' level of a resource, the rate of increase of a consumer population would be zero (Caughley & Lawton 1981). In the present study, as well as in other studies (J. Caughley *et al.* 1984; Bayliss 1985b, 1987), the resource of plant biomass (and primary production) has been related to a rainfall index. For red kangaroos in the South Australian pastoral zone, the amount of summer–autumn rainfall required for the yearly exponential rate of population increase to equal zero was found to be lower in the Western management zones that it was in the Central & Eastern management zones (Fig. 4). J. Caughley *et al.* (1984) also found that a regional (east–west) difference in the amount of rainfall required for the rate of population increase to equal zero existed for both red and grey kangaroos in western New South Wales. This difference was attributed to recognizable soil and plant community differences between higher and lower rainfall regions (J. Caughley *et al.* 1984). In South Australia, however, because the most common soil types and plant communities are found throughout the pastoral zone (Laut *et al.* 1977), such a conclusion as to the regional differences in the amount of summer–autumn rainfall required for 'equilibrium' was considered unlikely.

Explicit models such as the Mitscherlich equation have been described as consonant models: models for which the structure, as well as the predictive outcome, agree with reality (Caughley 1981). Bayliss (1985b, 1987) suggested interpretations of the constants of both the Michaelis-Menten equation and the Mitscherlich equation. For the Mitscherlich equation, in the form used in the present study, Bayliss' (1987) equivalent definitions of the constants were that 'a' is equivalent to the maximum rate of population increase, 'b' is equivalent to the rate at which the maximum rate of population decline in the absence of resources (a−b) is ameliorated by increasing resources, and 'k' is equivalent to a term described as demographic efficiency. If these consonant definitions for the Mitscherlich equation are to be used to interpret the numerical response of kangaroo populations in relation to changing levels of a resource, or some index of it, then some care must be exercised, particularly since the coefficients 'b' and 'k' of this model are highly correlated (Digby, Galwey & Lane 1989) and can therefore assume a number of values when fitted using the method of maximum likelihood.

According to Bayliss (1987), the consonant definition of the asymptote of the Mitscherlich equation (a) is the maximum rate of population increase. This is presumed to be a generic maximum rate and not necessarily the intrinsic (maximum) rate of population increase defined by Caughley & Birch (1971) for a population with a stable age distribution and unlimited resources. For red kangaroos at Kichega National Park, this aymptotic maximum value of r was estimated to be in the range 0·34−0·58 (Bayliss 1985b, 1987). For red kangaroos on the inland plains of western New South Wales, equivalent estimates of this maximum value of r were 0·26 and 0·33 (J. Caughley *et al.* 1984). Bayliss (1985b) also derived a number of maximum yearly rates of population increase for red kangaroos (intrinsic and otherwise) from model life-tables with both stable and unstable age distributions, and from Caughley & Krebs' (1983) body weight formula. The maximum rates derived this way were 0·41−0·44 for populations with stable age distributions, and 0·57−0·67 for populations with unstable age distribution (Caughley & Krebs 1983).

At 0·38, the asymptotic maximum value of r for the red kangaroo populations in the Central and Eastern kangaroo management zones was similar to those estimated for populations in western New South Wales, and near to the theoretical values derived by Bayliss (1985b) for populations with stable age distributions. At 0·92, the asymptotic maximum value of r for the red kangaroo populations in the Western kangaroo management zones was much higher than even the derived values for populations with unstable age distributions. Even taking into account the relatively large standard errors of both estimated asymptotic maximum values of r (Table 5), it would appear that the populations of the Western kangaroo management zones were likely to be far less constrained in their response to the 'boom' conditions that could be initiated by high summer−autumn rainfall than perhaps were other kangaroo populations.

As was the case in the two studies conducted in western New South Wales (J. Caughley *et al.* 1984; Bayliss 1985b, 1987), the two models of the numerical response of red kangaroo populations to rainfall proposed in the present study were developed using data from a series of good seasons followed by a drought. Subsequent predictions made using these models of the responses of the red kangaroo populations to summer−autumn rainfall in the period 1984−88 were found to be at considerable variance to reality (Fig. 5). A reason for this might be that rainfall is just a poor predictor of the behaviour of red kangaroo populations, regardless of the form of the model into which it is incorporated. An alternative hypothesis, however, that might explain this is that the age distributions and sex ratios of the post-drought populations were considerably different to those of the populations used to develop the models; this leading to different behaviour as far as the response to rainfall and its effect upon food availability is concerned. Such a proposition is not entirely implausible. Bayliss (1985b) has shown that alteration of the age distribution of a red kangaroo population can alter the maximum rate of population increase.

Following the drought, the kangaroo populations in South Australian pastoral zone reached their lowest numbers since 1978. The age structures of these populations were assumed to have been truncated through heavy juvenile mortality and, to a lesser extent, heavy mortality in the oldest age-classes. The sex ratios of these populations were also assumed to be female-biased as a result of heavier mortality in males than females. Such was the impact of the drought upon the kangaroo populations of Kinchega National Park in western New South Wales (Robertson 1986). If this had happened, then the age structures would have been unstable; biased towards the most fecund female age-classes. A consequence of such a situation could be to increase the level of the numerical response above that which would be characteristic of a population near to the carrying capacity of its environment with an age distribution tending towards stability. From Fig. 5 it would appear that the numerical responses to the rainfall index following the drought had shifted down the rainfall (resource) axis; at least for the immediate post-drought years of 1985−86. The numerical response of red kangaroo populations in South Australia to resource availability may occupy several positions in relation to a resource axis, depending upon population density, age structure and sex ratio (Cairns 1989).

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Appendix 1

The number of red kangaroos (±SE%) in each of the 10 SANPWS kangaroo management zones plus the pastoral zone totals (zone 5a excluded) for the period 1978–88.

	1978	1979	1980	1981	1982	1983
1	99 400 ± 13%	138 900 ± 15%	92 900 ± 18%	155 100 ± 1%	208 100 ± 15%	111 300 ± 21%
2	28 800 ± 8%	88 700 ± 4%	71 300 ± 7%	203 300 ± 3%	198 300 ± 10%	55 800 ± 9%
3	66 100 ± 15%	97 700 ± 14%	106 700 ± 14%	173 700 ± 10%	167 500 ± 15%	88 200 ± 10%
4	35 700 ± 12%	40 100 ± 10%	41 900 ± 12%	51 100 ± 17%	23 700 ± 12%	26 400 ± 8%
5a			Not surveyed			8 600 ± 47%
6	220 300 ± 6%	259 400 ± 12%	185 400 ± 10%	399 900 ± 10%	92 100 ± 9%	49 200 ± 23%
7	129 100 ± 22%	146 800 ± 10%	177 500 ± 14%	326 700 ± 9%	170 300 ± 9%	134 500 ± 15%
8	360 500 ± 14%	302 800 ± 15%	387 600 ± 19%	793 900 ± 12%	437 400 ± 18%	292 000 ± 13%
9	60 100 ± 27%	45 100 ± 27%	73 800 ± 31%	71 300 ± 43%	65 700 ± 58%	47 200 ± 36%
10a	0	0	500 ± 60%	200 ± 50%	0	0
Total	1 000 000 ± 6%	1 119 500 ± 6%	1 137 600 ± 8%	2 175 200 ± 5%	1 363 600 ± 7%	804 600 ± 7%

	1984	1985	1986	1987	1988
1	74 500 ± 15%	161 600 ± 21%	145 300 ± 11%	94 100 ± 12%	144 100 ± 18%
2	106 600 ± 7%	182 900 ± 11%	137 100 ± 13%	103 000 ± 7%	140 700 ± 8%
3	66 000 ± 12%	127 900 ± 13%	111 100 ± 15%	117 600 ± 12%	132 200 ± 17%
4	41 900 ± 13%	27 900 ± 9%	49 800 ± 13%	40 900 ± 15%	43 200 ± 21%
5	2 500 ± 72%	200 ± 100%		Not surveyed	
6	106 600 ± 11%	161 900 ± 7%	237 000 ± 10%	108 200 ± 7%	230 400 ± 10%
7	80 100 ± 13%	128 500 ± 13%	125 000 ± 10%	119 200 ± 10%	166 300 ± 11%
8	213 800 ± 14%	313 600 ± 26%	276 200 ± 22%	307 100 ± 13%	509 500 ± 15%
9	53 000 ± 26%	25 700 ± 34%	43 400 ± 12%	65 400 ± 25%	90 600 ± 12%
10a	2 600 ± 12%	9 700 ± 40%	5 000 ± 42%	7 800 ± 53%	Not surveyed
Total	745 100 ± 5%	1 139 700 ± 8%	1 129 900 ± 6%	963 300 ± 5%	1 457 000 ± 6%